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The Internet of Plants: Re-Imagining Plant Signalling Networks Through an Information-and-Communication Theory Lens

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Abstract

Plants are dynamic, responsive systems capable of perceiving, integrating, and transmitting information across multiple scales, from molecular pathways within cells to complex interactions at the community level. Emerging evidence demonstrates that plants employ diverse signalling modalities, including electrical, chemical, hydraulic, and volatile signals, which operate simultaneously and synergistically to coordinate behaviour. Inspired by advances in network science and information theory, this mini-review proposes a conceptual framework for understanding plant signalling as a distributed, multi-layered communication network: an "Internet of Plants." We discuss the potential of applying information and communication theory (ICT) metrics to quantify signal generation, transmission, fidelity, and network efficiency. This mini-review highlights new research avenues in integrative plant biology, including predictive modelling of signal flow, the role of environmental noise, and the functional implications of inter-plant networks mediated by mycorrhizae and volatiles. By framing plant signalling through an ICT lens, we aim to unify molecular, organ-level, and ecological studies into a cohesive theoretical framework that can guide future experimental and computational research. By turning a popular metaphor into a quantitative, falsifiable program, this mini-review connects molecular signalling with whole-plant physiology and community dynamics, enabling cross-species comparisons and reproducible benchmarks.

Keywords

information theory, calcium signalling, electrophysiology, volatile organic compounds, mycorrhizal networks, plant communication

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1. Introduction: Beyond the Metaphor

Plants are highly dynamic biological systems that continuously perceive and integrate environmental information across spatial and temporal scales. This responsiveness depends on interacting signalling pathways, including calcium (Ca^{2+}), reactive oxygen species (ROS), volatile organic compounds (VOCs), hormonal, electrical, hydraulic, and chemical cues.[1-4]

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These signalling systems coordinate networks that connect local perception with systemic physiological adjustment, enabling plants to integrate abiotic stress, herbivory, pathogen challenge, and developmental cues into coherent responses.[1-7]

Long-distance and systemic signalling are now well established as central features of plant function. Root-to-shoot communication integrates multiple mobile molecules and pathways to coordinate whole-plant responses,[6] while electrical and Ca^{2+} signals can propagate rapidly across tissues following wounding, herbivory, or other disturbances.[2,3,8-10] Hormonal signalling further provides spatially and temporally organized control over growth, defence, and adaptation[4,5,7,11] and plasmodesmata and vascular tissues constitute essential anatomical substrates for intercellular and long-range information transfer.[12,13] Beyond the individual plant, communication also extends into the rhizosphere and surrounding community through VOCs, root exudates, and mycorrhizal associations, which influence neighbouring plants, microbes, and broader ecological interactions.[14-18] Collectively, these studies support the view that plants should not be understood merely as collections of biochemical pathways, but as integrated signalling systems with distributed information-processing properties.

At the same time, the language used to describe plant communication has often remained metaphorical. Terms such as "plant communication," "wood-wide web," and related network analogies have been useful for drawing attention to the complexity of plant interactions, but they have also generated conceptual ambiguity and, in some cases, overinterpretation.[17,19,20] In particular, debate around the generality and mechanistic interpretation of common mycorrhizal networks highlights the need for greater analytical precision and stronger criteria for distinguishing evocative metaphor from testable biological mechanism.[17,20] Thus, while the idea of an "Internet of Plants" is appealing, its scientific value depends on whether it can be translated into a rigorous framework grounded in measurable signalling processes, network structure, and quantifiable information transfer.

This is where information theory and network science become especially relevant. These mathematical traditions have long been used to study how complex systems encode, transmit, filter, and recover information under constraints such as noise, limited capacity, redundancy, and energetic cost. In plant systems, related ideas have already begun to emerge. Studies of Ca^{2+} oscillations show that signal frequency and amplitude can encode biologically meaningful information.[4,21] Work on stress signalling and defence pathways demonstrates that plants integrate multiple concurrent signals under noisy environmental conditions.[1-3,10,22] More broadly, information-theoretic analysis has been applied to biological signalling and plant specialized metabolism to examine trade-offs between fidelity, cost, and accuracy.[23,24] However, these insights remain scattered across subfields and are rarely synthesized into a unified framework that connects subcellular signalling, organ-level transport, whole-plant coordination, and ecological communication.

This mini-review addresses that gap by proposing the "Internet of Plants as a unified and testable framework for plant signalling research. By linking intracellular coding, intercellular transfer, vascular signalling, and ecological communication to concepts from information theory and network science, the framework provides a shared vocabulary and a quantitative basis for comparing signalling modes, evaluating robustness, and generating falsifiable hypotheses. We build on previous work in plant signalling, electrophysiology, hormone biology, and ecological communication,[2-4,6,8,12,16-18] while also incorporating critical caution from recent scholarship warning against overly broad claims about underground communication networks.[20] Our aim is therefore both synthetic and corrective: to unify diverse signalling literatures within a common framework while maintaining conceptual discipline about what is empirically established, what remains inferential, and what must still be tested. Thus, the present mini-review is not to claim that a complete plant information theory already exists, but to establish a quantitatively grounded and experimentally testable framework through which plant signalling can be analysed using explicit equations, measurable variables, comparative evidence, and falsifiable predictions.

In this framework, the present mini-review makes three main contributions. First, it proposes a multi-layer architecture linking intracellular encoding, intercellular transfer, vascular and organ-level signalling, and community-scale ecological communication. Second, it provides a direct mapping between concepts from information theory and network science and concrete plant structures and processes, including plasmodesmata, vascular strands, volatile diffusion, and mycorrhizal links. Third, it outlines a research agenda in which metrics such as entropy, mutual information, channel capacity, centrality, modularity, and efficiency can be translated into experimentally tractable hypotheses about plant stress perception, prioritization, robustness, and adaptation. In doing so, this manuscript seeks to situate plant signalling within a broader quantitative framework that can support cross-scale comparison, computational modelling, and falsifiable predictions.

For ease of reference, Table 1 summarizes key concepts from network science, computer networking, and information theory and shows how they may be interpreted in the context of plant communication.

Standard definitions are adapted from classical network science and information theory, while the plant-specific interpretations are derived from the present synthesis of literature on plasmodesmatal transport, vascular long-distance signalling, mycorrhizal networks, volatile/root-exudate communication, calcium/electrical signalling, hormone signalling, and information-theoretic analysis of biological signalling.[4,7,12-14,16,21,23-25]

Table 1. Summary of Core Concepts From Network Science, Computer Networking, and Information Theory, Showing Their Standard Definitions and How They Can be Interpreted in the Context of Plant Signalling and Communication Across Intracellular, Intercellular, Vascular, and Ecological Scales

Concept (ICT/info-theory)	Standard meaning	Plant communication interpretation	Key references
Node (vertex)	Entity that can send, receive, or relay information in a network	Cell, tissue region, organ (leaf, root, stem), entire plant, or mycorrhizal fungus individual acting as signalling units	[12,16,25]
Edge (link)	Connection along which information can flow	Plasmodesma, vascular strand (xylem/phloem segment), mycorrhizal hypha, or diffusion path for volatiles/root exudates	[12-14,16,18]
Network topology	Pattern of how nodes are interconnected	Leaf venation, root system architecture, plant–microbe interaction network, spatial arrangement of neighbouring plants	[14,16,17,25]
Degree/hub	Number of links per node; hubs have very high degree	Highly connected junctions in vascular tissue (root crown, stem branching points) or "hub" plants in a mycorrhizal network	[16,25]
Path/shortest path	Route (minimal hops) between two nodes	Fastest anatomical/ecological route for a signal to travel from one organ/plant to another	[2,13,16]
Centrality (degree, betweenness, closeness, eigenvector)	Measures of how "important" a node is for connectivity or information flow	Organs or plants predicted to be key coordinators of signalling; removal strongly affects propagation speed/extent	[16,25]
Channel	Physical/logical medium carrying signals	Individual vessel, plasmodesmatal corridor, mycorrhizal cord, or air/soil as medium for chemical cues	[12,13,16,18]
Bandwidth	Maximum rate at which information can be transmitted	Maximal rate of Ca^{2+} spikes, action potentials, or chemical pulses along a given tissue or hypha	[2,4,19,21]
Latency/jitter	Delay between sending and receiving; variability in that delay	Time (and its variability) between stimulus at one site and response at another organ/plant	[2,3,10]
Shannon entropy (H)	Average uncertainty/information content of a source	Diversity of possible signalling patterns (e.g. Ca^{2+} spike trains, volatile blends) across conditions	[21,23,24]
Mutual information (I)	How much knowing one variable reduces uncertainty about another	How well a signalling pattern predicts stimulus identity, intensity, or spatial origin	[23,24]
Channel capacity (C)	Maximum reliable information rate through a noisy channel	Upper bound on bits per unit time that a vascular path or mycorrhizal link can carry, given noise and biophysical constraints	[23,24]
Redundancy	Repetition that improves robustness at the cost of efficiency	Use of multiple concurrent modalities (electrical, Ca^{2+}, hormonal, volatile) to encode overlapping information	[2-4,7,10,19]

In a typical experiment, a localized stimulus, such as mechanical wounding, herbivore simulation, salt stress, or localized heat, can be applied at a known time and position, while distal tissues are monitored using surface electrodes, calcium reporters, ROS-sensitive probes, hormone reporters, or volatile-collection systems. In this framework, latency is the elapsed time between stimulus onset and the first detectable response in a distal tissue, while jitter is the variation in that delay across repeated trials, organs, or genotypes. Propagation velocity may be estimated from travelled distance divided by response time, allowing comparison of signalling efficiency across pathways such as vasculature, plasmodesmata-linked tissues, or mycorrhizal connections. Bandwidth can be operationalized as the effective rate at which distinguishable signal events or states, for example calcium spikes of different frequencies, electrical impulses, or chemical pulses, can be transmitted and reliably resolved per unit time. In practice, this can be estimated from time-series data by determining how many discrete signal states remain separable above noise within a defined temporal window. Thus, these metrics are not intended as abstract metaphors, but as measurable descriptors that can be extracted from real-time plant signalling experiments and compared across stimuli, pathways, and environmental conditions.

2. From Biochemical Pathways to Information Networks

Classical studies in plant biology have long mapped the intricate networks of biochemical signalling that underpin plant responses to their environment. Phytohormones such as auxin, abscisic acid (ABA), ethylene, jasmonic acid (JA), and salicylic acid (SA) orchestrate developmental processes and stress responses, while reactive oxygen species (ROS) and calcium (Ca^{2+}) waves provide rapid intracellular and intercellular signalling.[26] Complementing these chemical signals, plants generate electrical potentials and employ hydraulic cues to coordinate responses across tissues, integrating environmental information over spatial and temporal scales.[5] For example, in *Arabidopsis thaliana*, local wounding of leaves triggers systemic jasmonate accumulation and electrical signals that propagate along the vasculature within seconds to minutes, altering gene expression in distal tissues; similar long-distance electrical and Ca^{2+} waves have been recorded in tomato, lima bean, and poplar under herbivory and drought.[9] Volatile organic compounds (VOCs) and root exudates further extend communication beyond the individual, mediating interactions with neighbouring plants, symbiotic microbes, and herbivores.[14,15]

Viewed through an information-theoretic lens, these pathways can be conceptualized as components of a distributed communication system. Each signalling molecule or electrical spike represents a discrete unit of information, transmitted from a source (cell or organ) through a channel (such as plasmodesmata, vascular tissue, extracellular space) to a receiver (target cells or neighbouring plants). Noise arising from environmental variability or stochastic biochemical processes challenges signal fidelity, while feedback mechanisms and signal redundancy serve as biological error-correction strategies.

Some research highlights that long-distance signalling, such as systemic acquired resistance or wound-induced electrical waves, mirrors network synchronization phenomena observed in engineered systems.[2,10] The integration of multiple signal modalities such as chemical, electrical, hydraulic demonstrates the plant's ability to process and encode information, much like a distributed computing system balancing multiple data streams.[3] Recent experimental work provides evidence of long-distance signal coordination. For example, systemic acquired resistance (SAR) demonstrates how local pathogen recognition triggers molecular cascades that propagate signals throughout the plant, priming distal tissues for defence.[11,26] Similarly, electrical and Ca^{2+} waves can transmit information at high speed between leaves and roots, coordinating rapid responses.[22] These examples suggest that plant signalling networks possess features akin to engineered information systems: nodes (cells/organs), edges (signal pathways), and dynamic feedback loops. By mapping biochemical pathways onto an information network framework, we can begin to quantify signal flow, evaluate efficiency, and predict behavioural outcomes at both the organismal and community levels.

3. Architectural Principles of the "Internet of Plants"

The "Internet of Plants" can be conceptualized as a multilayered network, where information is processed, integrated, and transmitted across different organizational scales. At the intracellular level, signalling cascades comprising transcription factors, secondary messengers, and metabolic intermediates enable cells to sense local conditions and coordinate internal responses.[3] Cells communicate with neighbours through plasmodesmata, electrical coupling, and paracrine chemical signals, forming intercellular networks that synchronize responses across tissues.[12] At the organ level, vascular tissues facilitate long-distance communication, transmitting hydraulic signals, electrical potentials, and hormone fluxes between roots, shoots, and leaves. This integration allows the plant to rapidly adjust stomatal behaviour, resource allocation, and growth patterns in response to environmental changes.[13] Beyond the individual, plants interact with external networks through mycorrhizal connections, root exudates, and volatile organic compounds, effectively exchanging information with neighbouring plants, symbiotic microbes, and herbivores.[14,16] These multi-organ and multi-species networks resemble distributed communication systems, where each node (cell, organ, or plant) processes and relays information while contributing to system-wide behaviour.

Applying concepts from network science, these signalling layers can be analyzed in terms of modularity, connectivity, redundancy, and centrality. For example, measures such as centrality identify highly connected "hub" organs such as roots or meristems which may coordinate systemic responses, modularity captures functionally distinct subnetworks, and redundancy reflects signal robustness against perturbations. Network efficiency can be assessed through metrics analogous to bandwidth and latency, capturing how rapidly and reliably signals propagate under environmental constraints. Such a framework not only clarifies how plants achieve coordinated behaviour but also provides a quantitative basis for predicting responses to perturbations, from abiotic stress to pathogen attack.

By framing plant signalling as an interconnected information network, we move closer to a systems-level understanding of plant behaviour, integrating molecular mechanisms with organ-level dynamics and ecological interactions. This perspective lays the foundation for treating plants not merely as passive responders but as active information-processing networks, capable of sophisticated communication both within themselves and with their environment. Moreover, each plant organ can

be treated as a "node" with local processing capabilities, integrating inputs from multiple channels before generating outputs. This perspective facilitates computational modelling of systemic behaviours, such as resource allocation, stress tolerance, and coordinated defence, within and between plants.

It is important to emphasize that the signalling layers described in this framework should not be interpreted as isolated or strictly modular channels. In living plants, communication emerges from strongly interconnected and nonlinear crosstalk among Ca^{2+}, ROS, electrical, hydraulic, hormonal, and metabolic pathways, with the functional meaning of any one signal depending on developmental state, tissue identity, prior stress exposure, resource status, symbiotic context, and environmental conditions. Feedback regulation and cross-pathway coupling therefore do not merely modify signalling outcomes but are intrinsic to how plant information is generated, filtered, and interpreted.[4,7,22,27] For this reason, terms borrowed from computer networking are used here as analytical tools rather than literal one-to-one biological equivalents. The same caution applies at the ecological scale. Volatile- and mycorrhiza-mediated interactions may support information transfer under some conditions, but the degree of coordination, routing specificity, and community-level integration is likely to be highly context dependent and remains debated, particularly for common mycorrhizal networks.[17,18,20] Likewise, signalling fidelity must be considered together with energetic and ecological trade-offs, since greater redundancy or higher-information signals may improve robustness while also increasing metabolic cost.[23,24] In this revised sense, the "Internet of Plants" is best understood as a flexible and testable framework for analysing coupled, context-sensitive signalling systems, not as a claim that plant communication behaves like a fully modular engineered network.

4. Coding, Noise, and Feedback in Plant Communication

In engineered communication systems, information is encoded, transmitted through channels, and decoded at the receiver, all while contending with noise and signal degradation. This mapping can be formalized by treating plant signalling modalities as stochastic communication channels in the Shannon sense, with defined input distributions (environmental stimuli), conditional output distributions (observed signalling patterns), and channel capacity and mutual information as quantitative measures of how efficiently and faithfully different tissues or pathways transmit information. Analogously, plants appear to employ sophisticated biological coding strategies to transmit information with high fidelity across cellular, organ, and organismal networks. Calcium oscillations, ROS bursts, and electrical spikes can function as temporal or frequency-based codes, conveying the intensity, duration, and type of environmental stimuli.[4] Hormonal gradients similarly encode developmental and stress-related information, with spatial and concentration patterns interpreted by downstream signalling modules.[7]

Environmental variability, stochastic biochemical fluctuations, and cross-talk between signalling pathways introduce noise, potentially distorting information flow. Plants mitigate these challenges through feedback loops, redundancy, and signal integration. For instance, stomatal regulation exemplifies a feedback-controlled system: hydraulic and hormonal signals continuously adjust guard cell behaviour to maintain optimal water balance.[27] Similarly, wound-induced ROS and Ca^{2+} waves encode spatial and temporal information about the injury, allowing distal tissues to mount appropriate defence responses.[10] Such mechanisms resemble error-correction protocols in digital networks, ensuring reliable communication despite intrinsic and extrinsic noise. Moreover, plants appear to encode signals according to urgency and relevance, suggesting a form of dynamic bandwidth allocation, where limited resources are optimally distributed to process critical information.[19]

Adopting an information-theoretic perspective allows quantitative evaluation of signalling efficiency, reliability, and robustness. Metrics such as signal-to-noise ratio, information entropy, and redundancy could provide novel insights into how plants encode environmental cues and coordinate systemic responses. This framework not only illuminates the functional sophistication of plant signalling but also enables predictive modelling of behaviour under diverse environmental scenarios, bridging the gap between molecular pathways and emergent, network-level phenomena. Additionally, information-theoretic metrics such as Shannon entropy can be used to quantify the information content of plant signalling patterns. For instance, the information carried by Ca^{2+} spike frequency versus amplitude, or by volatile blends of differing complexity, and also to quantify trade-offs between metabolic cost, robustness, and precision in plant communication. High-entropy signals generally carry more information but are expected to incur higher energetic costs, whereas low-entropy signals can be faster and metabolically cheaper at the expense of precision.[23,24] Understanding this trade-off could illuminate evolutionary strategies in plant signalling networks.

In this framework, biological error mitigation in plants can be conceptualized as a six-step process through which signalling fidelity is maintained under noisy conditions. First, the plant encodes a stimulus into structured signals, such as Ca^{2+} oscillation frequency, ROS pulse timing, electrical depolarization, or hormone gradients, rather than relying on a single undifferentiated output.[4,7,21] Second, that information is transmitted through multiple partially overlapping channels, including plasmodesmata, vascular tissues, extracellular chemical diffusion, and in some cases volatile or mycorrhizal

pathways, which reduces the chance that one disturbed route will fully erase the message.[12,13,16] Third, local relay tissues and receiver cells integrate incoming signals and can amplify biologically important patterns, as seen in wound-induced electrical and Ca^{2+} waves that propagate from a local injury to distal tissues.[2,3,10] Fourth, feedback loops continuously compare internal state with ongoing inputs and adjust the response, thereby limiting signal drift; stomatal control under fluctuating water status provides a clear example of such feedback regulation.[27] Fifth, redundancy across signalling modalities acts like biological fault tolerance: if one signal becomes weak or noisy, overlapping information carried by electrical, calcium, ROS, hydraulic, or hormonal pathways can still preserve the functional meaning of the message.[1,2,4,22] Sixth, receiver tissues effectively decode the signal by integrating signal strength, duration, timing, and spatial pattern, allowing the plant to distinguish among stress classes and mount an appropriate response rather than reacting indiscriminately.[4,7,23,24] In this sense, plants do not maintain signalling fidelity through a centralized digital protocol, but through distributed filtering, redundancy, feedback stabilization, and multi-signal integration. Together, these processes provide a biologically plausible analogue of error control in a noisy communication network. In network terms, this sequence corresponds to encoding, multi-path transmission, relay and amplification, feedback-based correction, redundant backup signalling, and context-dependent decoding at the destination tissue.

5. The Mycorrhizal-Internet and Ecological Communication

Beyond intra-plant networks, plants participate in inter-organismal communication networks that span entire ecosystems. One of the most compelling examples of inter-plant communication is the mycorrhizal network, often termed the "wood-wide web." The mycorrhizal network, an intricate web of fungal hyphae connecting multiple plant species serves as a natural prototype of the "Internet of Plants," facilitating the transfer of nutrients, chemical signals, and potentially RNA molecules across individual organisms. These underground networks have been proposed to facilitate the transfer of resources and signalling cues, potentially contributing to community-level interactions under certain conditions.[17] These exchanges may be usefully analysed through analogies to routing in networked systems, but such comparisons remain provisional because the specificity and generality of common mycorrhizal network-mediated signalling are still debated, including by Karst et al[20]

Experimental evidence shows that plants connected through mycorrhizae can detect herbivore attack on a neighbour and preemptively upregulate defensive pathways. Volatile organic compounds (VOCs) and root exudates complement these fungal connections, enabling plants to communicate with neighbours without direct physical contact. For example, VOCs released upon herbivory can prime defence responses in nearby conspecific or heterospecific plants, enhancing the resilience of the plant community.[18] Root exudates can similarly influence microbial communities and neighbouring roots, modulating nutrient uptake, growth, and pathogen resistance.[14]

Applying an information-network perspective, these inter-plant interactions can be framed as biological communication protocols, with nodes (individual plants) exchanging packets of information via multiple channels (fungal hyphae, volatiles, exudates). The topology and connectivity of these networks influence information dissemination, cooperative behaviour, and ecological stability. Highly connected "hub" plants, or keystone nodes, may be analysed as high-centrality nodes in some ecological contexts, amplifying signals and coordinating potential neighbour or network-level effects under specific conditions.[11] Viewing these interactions as integrated networks allows us to ask quantitative questions: How does network topology influence resilience to stress? Do plants prioritize certain connections for information flow? How does signal redundancy affect community stability?

Understanding the mycorrhizal internet as a structured signalling network offers a new lens to explore plant behavioural ecology, revealing how information flow shapes competition, cooperation, and adaptation in complex environments. It also highlights the potential for predictive modelling of ecosystem responses, where network disruption through habitat loss, climate change, or pathogen invasion can have cascading effects on community signalling and function.

6. Experimental Evidence Supporting the Framework

A key strength of the "Internet of Plants" framework is that several of its core components are already supported by experimental plant biology, although the evidence is stronger for some signalling layers than for others. Within individual plants, some of the clearest support comes from wound and stress experiments showing rapid systemic electrical and calcium signalling. Localized leaf damage in *Arabidopsis thaliana* can trigger rapid electrical activity and the systemic accumulation of jasmonates in distal tissues, demonstrating that information generated at one site is transmitted across the plant on biologically meaningful timescales.[2,9,10] In well-studied cases such as wound-induced electrical and Ca^{2+} waves, experimental evidence supports the existence of structured internal signalling pathways that enable long-distance coordination beyond isolated local responses.[2,3,22]

Additional experimental support comes from studies of intercellular transport and tissue-level connectivity. Plasmodesmata regulate molecular traffic between adjacent cells and provide a direct structural basis for cell-to-cell communication, making them strong biological analogues of short-range communication channels within a distributed network.[12] At a larger scale, vascular tissues mediate long-distance transport of signals, hormones, and stress-related cues between roots and shoots, providing an anatomical substrate for coordinated whole-plant signalling.[6,13] Together, these findings support the framework's treatment of cells, tissues, and organs as connected nodes linked by channels of differing range, speed, and selectivity.

Evidence also supports communication beyond the individual plant, although the strength and specificity of that evidence varies by signalling mode. Volatile-mediated plant-plant signalling is relatively well supported experimentally, especially in defence priming contexts where damaged plants emit volatile organic compounds that alter gene expression, defence status, growth, or reproduction in nearby receiver plants.[18] Root exudates likewise influence neighbouring roots and microbial communities, indicating that information exchange belowground can modify ecological interactions and resource dynamics.[14] These observations support the framework's extension from intra-plant to local ecological communication networks.

Additional support comes from studies of coding and response specificity. Calcium oscillations and ROS dynamics do not merely indicate generic activation, but can vary in amplitude, frequency, and timing in ways that reflect stimulus identity and physiological context.[1,4,21] Hormonal gradients similarly provide spatially organized information that guides development and stress adaptation. These observations are consistent with the manuscript's argument that plant signals may encode information in temporally and spatially structured forms, analogous to biological communication codes rather than undifferentiated stress outputs. Information-theoretic studies have already begun to test such ideas quantitatively, including work on signalling accuracy-cost tradeoffs in MAPK cascades and on information content in plant defence-associated metabolism.[23,24]

By contrast, evidence concerning common mycorrhizal networks remains more mixed and should be interpreted cautiously. Some studies support the idea that mycorrhizal connections can mediate the transfer of nutrients and warning-related signals among plants, consistent with a network-based model of community-level communication.[16,17] However, the magnitude, specificity, and generality of these effects remain debated, and some reported outcomes may also be explained by shared soil environments, diffusion processes, or experimental limitations rather than direct hyphal routing alone.[20] For this reason, the strongest current empirical support for the "Internet of Plants" framework lies in well-characterized intra-plant signalling systems and volatile-mediated neighbour effects, whereas some claims regarding highly specific underground inter-plant information routing remain provisional.

Collectively, these experimental findings justify the framework as more than metaphor. They show that plants possess identifiable signalling units, structured channels, long-distance propagation pathways, coded multi-modal responses, and ecologically relevant communication processes. At the same time, the evidence is uneven across scales, which reinforces the need for the quantitative approaches proposed later in this review to compare channel properties, signal fidelity, latency, redundancy, and network topology across distinct plant communication systems.

7. Toward a Quantitative "Plant Information Theory"

While conceptualizing plant signalling as an information network is compelling, a central challenge remains: how to measure and quantify information flow in living plants. Drawing from classical information and communication theory, we can begin to assign measurable parameters to plant signalling events, defining information units, estimating signal entropy, and evaluating network efficiency across scales. For example, the frequency and amplitude of calcium oscillations, ROS bursts, or electrical spikes could be treated as discrete bits of information, allowing quantitative comparisons between stimuli and responses.[21]

A simple illustrative example shows how this framework can operate in practice. Suppose a plant is exposed to three stimulus classes: herbivory, drought, and mechanical wounding. If each stimulus produces a distinct distribution of Ca^{2+} spike frequencies, then the uncertainty of the stimulus set can be expressed using Shannon entropy:

$$\mathrm{H}(S) = -\sum_{i=1}^{n} P(\mathrm{s}_i)\log_2\ p(\mathrm{s}_i)$$

where $p(s_i)$ represents the probability of each stimulus class. If the three stimuli are equally likely, then:

$$\mathrm{H}(S) = -3\left(\frac{1}{3}log_2\frac{1}{3}\right) = \log_2\ 3 \approx 1.585\ \text{bits}$$

This value represents the maximum uncertainty before any signal is observed. If the measured Ca^{2+} pattern reduces that uncertainty, then the information conveyed by the signal can be quantified as mutual information:

$$I(S\,;\,R) = H(S) \;-\; H(S\,|\,R)$$

where R is the observed response pattern. For instance, if the conditional uncertainty after observing the Ca^{2+} response is reduced to 0.40 bits, then:

$$I(S\,;\,R) = 1.585 - 0.40 = 1.185 \text{ bits}$$

indicating that the signalling pattern carries substantial information about stimulus identity. In biological terms, this implies that the plant response is not merely reactive, but sufficiently informative to discriminate among different environmental conditions.

The same logic can be extended to signal transmission across tissues. If a wound-induced electrical or Ca^{2+} signal travels from a damaged leaf to a distal leaf over a path length d in time t, the effective propagation velocity is:

$$v = \frac{d}{t}$$

Thus, if a signal traverses 12 cm in 30 s, then v=0.4 cm s^{-1}. Repeated measurements across organs or genotypes would allow estimation of mean latency, jitter, and transmission reliability. Likewise, if a signalling channel can reproducibly distinguish M discrete states per time interval Δt, its approximate information throughput can be expressed as:

$$C \approx \frac{log_2\ M}{\Delta t}$$

so that a pathway capable of transmitting four distinguishable signal states every 2 s would have an effective upper rate of:

$$C \approx \frac{log_2\ 4}{2} = \frac{2}{2} = 1\,\text{bit}\ \text{s}^{-1}$$

Importantly, this framework is not limited to hypothetical examples. Published datasets on wound-induced electrical and Ca^{2+} signalling in *Arabidopsis thaliana*, including those reported by Choi et al,[2] could be analysed by extracting spike-frequency or amplitude distributions across defined stimulus classes and then estimating entropy and mutual information to quantify signal discrimination. Such analyses would provide a practical route for testing how reliably plant signalling patterns encode stimulus identity, location, or intensity in real experimental systems.

Integrating network science provides additional analytical tools. Metrics such as node centrality, connectivity, modularity, and path length can quantify the roles of specific organs, tissues, or even individual plants in signal propagation. Long-distance signals, whether transmitted via vascular tissues or mycorrhizal networks, can be therefore analyzed not only for their biochemical identity, but also for their speed, reliability, redundancy, and topological importance, offering predictive insights into system behaviour under stress or perturbation.[25]

Recent advances in high-resolution electrophysiology, imaging technologies, and biosensors create opportunities to capture multi-modal signals simultaneously, enabling real-time mapping of information flow. Computational modelling, combined with machine learning approaches, could identify hidden patterns in signalling networks and predict emergent behaviour at organismal and community levels.[28]

Ultimately, a quantitative plant information theory would bridge molecular signalling with system-level and ecological dynamics, enabling a predictive framework for plant responses to complex environmental challenges. By treating plants as active information-processing systems, researchers can generate testable hypotheses about signal fidelity, network efficiency, resilience, and adaptation across scales.

8. Challenges and Future Directions

Despite the conceptual appeal of framing plant signalling as an information network, several critical challenges remain, offering opportunities for future research.

i. ***Defining measurable communication units***: Identifying standardized units of information, whether in chemical, electrical, or hydraulic signals, is essential for cross-study comparisons and quantitative modelling. Established toolkits from network science (centrality, modularity, and efficiency metrics) and information theory (entropy, mutual information, and channel-capacity estimation) offer immediately available quantitative formalisms that can be adapted to

plant electrophysiology, volatile signalling, and mycorrhizal communication without reinventing the underlying mathematics.

ii. ***Capturing multi-modal, real-time signalling***: Integrating chemical, electrical, hydraulic, and volatile signals simultaneously remains technically demanding, yet is crucial to understanding holistic plant communication.

iii. ***Scaling from cells to communities***: Current models largely focus on cellular or organ-level networks; extending these frameworks to whole-plant and inter-plant systems, including mycorrhizal networks, presents conceptual and computational challenges.

iv. ***Standardizing terminology across disciplines***: Bridging plant biology, network science, and information theory requires a common language for describing nodes, channels, signals, and information flow. Current claims are debated as Karst et al.[20] cited generality/over-interpretation.

v. ***Predicting system behaviour under perturbation:*** Understanding how plants maintain network robustness in response to environmental stressors, pathogens, or ecosystem disturbances is a key frontier.

vi. ***Ethical and conceptual considerations***: Ascribing concepts such as "communication" or "intelligence" to plants demands careful framing to avoid anthropomorphism while still acknowledging functional sophistication.

Addressing these challenges will require interdisciplinary collaboration, combining plant physiology, computational modelling, network science, and systems biology. By systematically exploring these frontiers, researchers can not only deepen our understanding of plant behaviour but also develop predictive frameworks for ecosystem management, crop resilience, and climate adaptation.

9. Conclusion

Reframing plant signalling as an "Internet of Plants" through the lens of information and communication theory offers a transformative perspective on plant biology. By conceptualizing plants as active, distributed information-processing systems, we can integrate molecular, organ-level, and ecological signalling into a unified framework. This approach highlights the remarkable sophistication of plant networks, from intracellular coding and feedback loops to inter-plant communication via mycorrhizal networks and volatile signals.

The "Internet of Plants" can serve as more than a metaphor when grounded in measurable signalling processes and testable quantitative hypotheses. By applying principles from network science and information theory, researchers can generate testable hypotheses about signal fidelity, network efficiency, resilience, and emergent behaviour. Such insights have profound implications, not only for fundamental plant biology but also for agriculture, ecosystem management, and climate adaptation strategies.

In sum, embracing this framework encourages a systems-level view of plant behaviour, challenging the perception of plants as passive organisms and positioning them as sophisticated communicators within their environment. As technological advances in sensing, imaging, and computational modelling continue to evolve, the vision of a fully mapped and quantitatively understood "Internet of Plants" moves closer to reality, opening new frontiers in plant science and ecological research. Understanding the "Internet of Plants" could illuminate how life optimizes information flow: from molecule to ecosystem, revealing a rich, interconnected world of plant behaviour waiting to be explored.

The "Internet of Plants" offers a structured framework for understanding plant signalling across molecular, organ-level, and ecological scales. Its value lies not in claiming that plant communication is already fully explained, but in providing measurable variables and shared analytical concepts, such as latency, redundancy, entropy, mutual information, and network topology, that can guide future experiments and models. Framed in this way, the concept moves beyond metaphor toward a falsifiable research program for quantitative plant communication biology.

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Additional data shall be made available by the author on request.

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